GENERAL NOTES

A RECONSIDERATION OF MIMICRY AND APOSEMATISM IN CATERPILLARS OF THE *PAPILIO MACHAON* GROUP

Williams (1966) pointed out that adaptation is a special and onerous concept that should only be invoked when other explanations have been ruled out by the evidence. To support a theory of Müllerian mimicry between taxa, the adaptive basis of mimetic resemblance (the color pattern, the defensive mechanisms that result in unpalatability) should be experimentally demonstrated. Correlated character distributions need not imply causal relationships (Miller & Wenzel 1995, Brower 1995), especially if complementary data on behavior and on interactions with predators in the field are subject to alternate interpretations (Lauder 1990). The burden of proof lies upon the advocate of a particular hypothesis of mimicry, because other, simpler explanations must be eliminated prior to acceptance of an adaptive scenario.

Mimicry among butterflies and day-flying moths is common, and its adaptive basis has been theoretically and empirically demonstrated (Bates 1862, Müller 1879, Brower 1958, Fisher 1958). Among lepidopteran larvae, however, the phenomenon is nearly unknown. Berenbaum (1995) recently reviewed three hypotheses to explain its apparent infrequency. First, evolution of larval patterns and colors could be limited by developmental constraints. That idea was rejected because there is genetic evidence for extensive larval pattern lability from the paradigmatic "model" lepidopteran, *Bombyx mori* L. Second, caterpillars may be less able than adults to survive handling by predators, as their bodies are more delicate (Poulton 1885) and they may suffer the additional risk of being knocked off their food plant. However, this hypothesis is not directly relevant to the evolution of mimicry, because it predicts that bright coloration attracting the attention of predators should be less likely to evolve in larvae, irrespective of their palatability or mimetic resemblances. Furthermore, the existence of many gaily-colored and noxious caterpillar species (Slater 1877, Bowers 1993, Sillén-Tullberg 1988) implies that fragility is not a major impediment to the evolution of bright larval color patterns.

A third possibility is that people simply have not noticed mimicry rings among caterpillars because immature Lepidoptera have not been as well studied as adults. We agree with Berenbaum that lack of study may partially explain the apparent rarity of larval mimicry in general, but we feel that an additional hypothesis may be relevant as well. We suggest that caterpillars do not commonly exhibit mimicry because they tend to be associated with particular foodplants which represent an "extended phenotype" (Dawkins 1982) that forms an integral part of potential predators' search image. If the plants look different, predators may be not be fooled by similarities in color pattern between potential models and mimics.

Berenbaum (1995) explored the idea that larvae of *Papilio polyxenes* Fabr. (Papilionidae) are Müllerian mimics with unpalatable larvae of *Danaus plexippus* L. (Nymphalidae). To support this hypothesis, *P. polyxenes* larvae must resemble monarch caterpillars closely enough that potential predators are deceived by their similarity, viewing larvae of both species as representatives of a single, noxious entity (Müller 1879). Additionally, *P. polyxenes* larvae must themselves be aposematic (unpalatable and warningly colored; Bowers 1993). In this note, we reevaluate the evidence supporting these two aspects of the hypothesized adaptive relationship between monarch and black swallowtail larvae. We question the view that larvae of *P. polyxenes* and its relatives are aposematic, and argue that this case of potential larval Müllerian mimicry is poorly supported by available evidence.

Is the larva of *P. polyxenes* unpalatable and warningly-colored? Many authors have contended that *P. polyxenes* (or its close relative *P. machaon*, and by extension, all *machaon*-group larvae) are aposematic. Because prey that are easy to see are more likely to be attacked by predators, aposematism will not evolve unless it confers an advantage greater than the cost of being obvious (Turner 1984). Here, we cast doubt upon the notion that *P. machaon*-group larvae are unpalatable in an ecologically meaningful sense,

contrary to the claims of Järvi et al. (1981), Sillén-Tullberg (1988, 1990), Berenbaum (1995), and others.

Recent support for the idea that these larvae are aposematic stems from a series of laboratory predation experiments testing ideas about kin selection and the evolution of gregariousness. In the first of these (Järvi et al. 1981), wild tits (*Parus*) were given a choice of halved mealworms (*Tenebrio*) and third-instar *P. machaon* larvae, after two initial trials with mealworms only. The birds ate only the mealworms and the authors concluded that the swallowtail larvae are unpalatable and supposed that they are also aposematic. However, as pointed out by Brower (1984), this experiment demonstrated neither unpalatability nor aposematism but simply a preference for familiar, palatable prey over novel, perhaps distinctly-flavored prey. Tinbergen (1960) found a substantial time lag between the advent of a novel prey species in the environment and its acceptance by tits, perhaps due to an innate avoidance of novel visual stimuli (Vaughan 1983) or to a failure to recognize the novel prey as food. The short duration of Järvi et al.'s experimental trials and the continual availability of a preferred alternative food weaken their conclusion that *P. machaon* larvae are unpalatable. However, the aposematism of *P. machaon* larvae was assumed in subsequent papers (e.g., Wiklund & Järvi 1982, Wiklund & Sillén-Tullberg 1985, Sillén-Tullberg 1988, 1990), and additional corroboration came only from indirect and uncontrolled observations, such as the low rate of attack on 6 to 7 cm. caterpillars by small birds (Sillén-Tullberg 1990) which might be frightened by the size of the "prey" alone. Stronger evidence for relative unpalatability among swallowtail larvae was provided by Leslie and Berenbaum (1990), who fed late instars of various species to quails (*Coturnix*) and found that both *P. polyxenes* and the cryptic *P. cresphontes* Cramer were always rejected whereas *P. glaucus* L. was always eaten.

It is likely that palatability of prey varies among predators (Poulton 1887, Brower et al. 1968) and also depends on the particular circumstances of the encounter (e.g., degree of hunger, availability of alternate prey; see Brower 1995). These experiments demonstrated that *P. machaon* and *P. polyxenes* larvae are not accepted by tits and quail under laboratory conditions (or simply that they not as tasty as mealworms or *P. glaucus* larvae). To make a convincing case for aposematism as an adaptive trait, however, experimental observations must be supported by evidence from the field, where the role of selection by birds can be evaluated in an appropriate behavioral and ecological context (Brower 1984, Takagi et al. 1995). Contrary to conclusions from the above experiments, evidence suggests that wild birds are important enemies of *P. machaon* larvae in nature. Dempster et al. (1976) recorded heavy predation by three passerine bird species at one site in Britain, and noted that the rate of bird attack was positively correlated with caterpillar density. This pattern is in accord with the search-image model of birds foraging for cryptic prey (Ruiter 1952, Tinbergen 1960), and would not be expected for an aposematic, unpalatable caterpillar. While comparable field observations have not been made for *P. polyxenes*, the food-plants, habitats, habits, and predator guilds of *P. machaon* and *P. polyxenes* are similar (Dempster et al. 1976, Feeny et al. 1985) and we would not expect these closely related species to differ greatly in susceptibility to birds.

Oviposition by *machaon*-group females and foraging behavior of larvae are also more consistent with their being palatable than aposematic. Nicholls and James (1996) reported relatively dispersed patterns of oviposition, with females often rejecting plants that already bore eggs; Evans (1984) was surprised to discover that supposedly aposematic *P. machaon* larvae are usually solitary (distribution significantly more uniform than a null hypothesis of Poisson distribution). Both observations imply a palatable larval lifestyle, for cryptic species tend to maintain low densities in the field to limit search-image formation by birds (Evans 1984), while many unpalatable larvae (including troidine swallowtails) are gregarious (Sillén-Tullberg 1988; although gregariousness is advantageous to aposematic caterpillars, some unpalatable species may be solitary, and cannibalistic, under certain circumstances, especially if they are competing for small food plants (Benson 1978)). Further, Codella and Lederhouse (1984) reported that *P. polyxenes* feeds so as to enhance crypsis, leaving symmetrical leaf damage and resting away from feeding areas (Heinrich 1979). In contrast, monarch larvae often feed in plain view on the upper surfaces of broad, leathery milkweed leaves.

Do the larvae of *Papilio polyxenes* mimic the larvae of *Danaus plexippus*? The

eight (Sperling 1987) to fourteen (Hancock 1983) species of the *Papilio machaon* group comprise a monophyletic lineage within the large genus *Papilio* (sensu Munroe 1961, Miller 1987, Sperling & Harrison 1994). The group has a Holarctic distribution apart from *P. polyxenes*, whose range extends to Ecuador (Tyler et al. 1994). Larvae feed primarily on the Apiaceae, a habit thought to have originated once, in the ancestor of the clade (Sperling & Feeny 1995). Like many swallowtails, the young larvae are dark with a white band, a pattern that may provide protection via resemblance to bird or lizard droppings (Minno & Emmel 1992). However, the later instars of all species in the machaon group share a color pattern not found elsewhere in *Papilio*—a distinctive display of green, black and white transverse annular stripes, some species with small orange or yellow spots scattered in the black (Igarashi 1979, Tyler et al. 1994). Berenbaum (1995) suggested that this pattern mimics the black, yellow and white rings of the unpalatable monarch caterpillar.

Because mimicry can evolve only when predators are exposed to both potential mimics and models (Sheppard 1960, Bowers 1988, Brower 1995), the hypothesis of mimicry between *P. polyxenes* and the monarch can be tested using cladistic and biogeographical evidence: if *machaon*-group larvae mimic *D. plexippus*, then their peculiar coloring must have arisen in sympatry with monarch larvae.Thus, if they are mimics, either *P. polyxenes* or *P. zelicaon* (because they are the only species in the machaon group with much geographical and ecological overlap with *D. plexippus*) must be the basal members of the clade, the Eurasian species having evolved later and retaining the mimetic color pattern in the absence of the model. Molecular data (Sperling 1987, Sperling & Harrison 1994), however, suggest that *P. alexanor* (from France, where no danaid species occurs) and *P. indra* (from the North American Great Basin, where the monarch occurs only rarely) are at the base of the *machaon* group. In any case, the conservatism of the pattern within the *machaon* group implies that it is unlikely to have originated via selection for mimetic resemblance to a species with which the majority of the taxa in the clade are largely or entirely allopatric. No alternative model has been suggested.

Monarch larvae could instead be mimics of *machaon*-group larvae, but we dismiss this suggestion because the monarch's larval color pattern occurs throughout *Danaus*. In fact, the details of the color patterns of some of the tropical *Danaus* species appear more similar to those of *P. polyxenes* than to the monarch's (Ackery & Vane-Wright 1984). Because there is even less geographical overlap between them, the chances for larval mimetic coevolution between species such as *D. erippus* and *D. chrysippus* and *machaon*-group caterpillars are less likely than is Berenbaum's monarch-*polyxenes* hypothesis.

Given these biogeographical arguments against mimicry in *machaon*-group caterpillars, we prefer E. B. Poulton's simpler explanation (1887, p. 240) "that the bright green coloring broken up by black markings is very well adapted for concealment among the much-divided leaves of the Umbelliferae on which the larva feeds." As pointed out by Endler (1978), crypsis does not demand dull coloration, but rather coloration that effectively matches the natural background (Poulton's [1884] "general protective mimicry"). A fat green caterpillar is not well hidden on a thin green leaf. The disruptive contrasting stripes on *machaon*-group caterpillars may be the most cryptic option given the architecture of the food plants and the constraints of body shape and size. An independent case of larval color-pattern change in concert with the host shift from Rutaceae to Apiaceae has been described in the unrelated South African swallowtail *Papilio demodocus* (Clarke et al. 1963). Those authors interpreted the change from a typical solid green and brown *Papilio* caterpillar to a rather unusual and contrasting mottled yellow and brown as being due to selection for crypsis on the new food plant.

Another challenge to the case for mimicry between *D. plexippus* and *P. polyxenes* larvae is suggested by the study of Heinrich and Collins (1983). Chickadees (*Parus atricapillus*) in an experimental aviary were able to recognize differences among plant species and to concentrate their search for prey on "host" plants while avoiding plant species that harbored no potential prey. We suggest that this sort of hierarchical searching in the wild may represent an integral part of the predator-prey signal system for aposematic larvae, and that birds are likely to learn not only the color pattern of the caterpillar, but also the architecture of its foodplant, as elements of the aposeme. If such discrimination among hunting sites is typical of foraging wild birds, then the chances of birds' mistaking a swallowtail

caterpillar on an umbellifer for a monarch caterpillar on a milkweed seem rather small, especially given the behavioral differences noted above. Mimicry between aposematic caterpillars sharing the same food plant (e.g., *Meris alticola* and *Neoterpes graefiaria* on *Penstemon* (Poole 1970, Stermitz et al. 1988) and *Eueides* and *Heliconius* on *Passiflora* (Brown & Benson 1975)) has a better chance of deceiving birds that use environmental cues to hierarchically focus their foraging behavior.

Although the proponents of the aposematism hypothesis generally concede that *P. polyxenes* and *P. machaon* larvae are extremely difficult to find in the field, many authors rationalize this apparent contradiction with the idea that *machaon*-group larvae are cryptic from a distance but warningly-colored at close range (e.g., Järvi et al. 1981, Lederhouse 1990, Brakefield et al. 1992, Takagi et al. 1995, Berenbaum 1995). This concept is referred to as "dual signals" by Rothschild (1975) and developed at greater length by Brown (1988). Given our hierarchical searching hypothesis, however, we feel that the dual signals concept applies better to aposematic adult butterflies and their mimics than it does to sedentary prey like caterpillars. Butterflies are mobile and may be encountered fortuitously anywhere in their habitat, which makes them relatively unpredictable prey. Predators of flying insects may pursue all of them by default, and rely on visual cues to break off an energetically expensive pursuit when the game is not worth the chase. By contrast, many caterpillars, including *P. machaon* group swallowtails, are sedentary on one or a few related host-plant species, and a fundamental component of finding and recognizing caterpillars as prey is finding their specific habitat. We thus view the dual-signals hypothesis to be less appropriate for larvae, and in particular for *P. machaon* group larvae, given Poulton's alternative explanation for the color pattern discussed above.

In conclusion, distinctive coloration as perceived by the human eye is not adequate evidence for adaptive function to the organism bearing it; aposematic warning is a possible but not necessary function of a color pattern. The monarch is a conspicuous feeder on a broad-leafed plant, suggesting that it maximizes the potential of the banded color pattern to function as a signal to predators. The black swallowtail's similar pattern is not displayed in this way, but instead in a manner consistent with a cryptic habit. This might be expected, because mortality data from the field suggest that the taste of machaon-group larvae is not broadly deterrent to avian predators. We consider *P. polyxenes* caterpillars to have the plesiomorphic color pattern for the machaon clade, and we consider crypsis the plesiomorphic function of the color pattern, because it evidently evolved along with a transition to herb-feeding. If evidence demonstrated both that *P. polyxenes* caterpillars in nature were unpalatable and that they behaved conspicuously, we would accept that the species had acquired a derived warning function for its larval coloring consistent with aposematism (an exaptation sensu Gould & Vrba 1982; see also Lauder 1990, Wenzel 1992). Were experimental data to show that birds avoid *P. polyxenes* under natural circumstances *because it looks like D. plexippus* (or some other model), only then would we conclude *that P. polyxenes* has gained a derived, adaptive function—mimicry—for its plesiomorphic coloration. We are doubtful that this will be demonstrated, and therefore argue that *P. polyxenes* is neither a Batesian nor a Müllerian mimic, but a relatively palatable caterpillar that relies on crypsis as its main defense from vertebrate predators in nature. The simplest explanation is that its coloring is disruptively cryptic, and that its resemblance to the monarch caterpillar is incidental.

LITERATURE CITED

ACKERY, P. R. & R. I. VANE-WRIGHT. 1984. Milkweed butterflies. British Museum (Natural History), London.

BATES, H. W. 1862. Contributions to an insect fauna of the Amazon Valley. Lepidoptera: Heliconidae. Trans. Linn. Soc. 23:495–566.

BENSON, W. W. 1978. Resource partitioning in passion vine butterflies. Evolution 32:493–518.

BERENBAUM, M. R. 1995. Aposematism and mimicry in caterpillars. J. Lepid. Soc. 49:386–396.

BOWERS, M. D. 1988. Plant allelochemistry and mimicry, pp. 273–311. In Barbosa, P. & D. K. Letourneau (eds.), Novel aspects of plant-insect interactions. John Wiley & Sons, New York.

———. 1993. Aposematic caterpillars: lifestyles of the warningly-colored and unpalatable, pp. 331–371. In Stamp, N. E. & T. M. Casey (eds.), Caterpillars. Chapman & Hall, New York.

BRAKEFIELD, P. M., T. G. SHREEVE & J. A. THOMAS. 1992. Avoidance, concealment, and defence, pp. 93–119. In R. L. H. Dennis (ed.), The ecology of butterflies in Britain. Oxford Univ. Press, Oxford.

BROWER, A. V. Z. 1995. Locomotor mimicry in butterflies? A critical review of the evidence. Phil. Trans. R. Soc. Lond. B 347:413–425.

BROWER, J. V. Z. 1958. Experimental studies of mimicry in some North American butterflies. Part I. The monarch, *Danaus plexippus* and the viceroy, *Limenitis archippus archippus*. Evolution 12:32–47.

BROWER, L. P. 1984. Chemical defence in butterflies, pp. 109–134. In Ackery, P. & R. I. Vane-Wright (eds.), The biology of butterflies, 2nd ed. Academic Press, London.

BROWER, L. P., W. N. RYERSON, L. L. COPPINGER & S. C. GLAZIER. 1968. Ecological chemistry and the palatability spectrum. Science 161:1349–1351.

BROWN, K. S., JR. 1988. Mimicry, aposematism and crypsis in neotropical Lepidoptera: the importance of dual signals. Bull. Soc. Zool. Fr. 113:83–101, pl. 1–16.

BROWN, K. S., JR. & W. W. BENSON. 1975. The heliconians of Brazil (Lepidoptera: Nymphalidae). Part VI. Aspects of the biology and ecology of *Heliconius demeter*, with description of four new subspecies. Bull. Allyn Mus. 26:1–19.

CLARKE, C. A., C. G. C. DICKSON & P. M. SHEPPARD. 1963. Larval color pattern in *Papilio demodocus*. Evolution 17:130–137.

CODELLA, S. G. & R. C. LEDERHOUSE. 1984. Foraging strategy and leaf damage patterns of black swallowtail caterpillars, *Papilio polyxenes*. Bull. New Jersey Acad. Sci. 29:37.

DAWKINS, R. 1982. The extended phenotype. Oxford Univ. Press, Oxford.

DEMPSTER, J. P., M. L. KING & K. H. LAKHANI. 1976. The status of the swallowtail butterfly in Britain. Ecol. Entomol. 1:71–84.

ENDLER, J. A. 1978. A predator's view of animal color patterns. Evol. Biol. 11:319–364.

EVANS, D. L. 1984. Ethology of defense in the aposematic caterpillar *Papilio machaon syriacus* (Papilionidae). J. Lepid. Soc. 38:194–201.

FEENY, P., W. S. BLAU & P. M. KAREIVA. 1985. Larval growth and survivorship of the black swallowtail butterfly in central New York. Ecol. Monogr. 55:167–187.

FISHER, R. A. 1958. The genetical theory of natural selection, 2nd ed. Dover Publications, New York.

GOULD, S. J. & E. VRBA. 1982. Exaptation—a missing term in the science of form. Paleobiol. 8:4–15.

HANCOCK, D. L. 1983. Classification of the Papilionidae (Lepidoptera): a phylogenetic approach. Smithersia 2:1–48.

HEINRICH, B. 1979. Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. Oecologia 42:325–337.

HEINRICH, B. & S. L. COLLINS. 1983. Caterpillar leaf damage and the game of hide-and-seek with birds. Ecology 64:592–602.

IGARASHI, S. 1979. Papilionidae and their early stages. Tokyo.

JÄRVI, T., B. SILLÉN-TULLBERG & C. WIKLUND. 1981. The cost of being aposematic: an experimental study of predation on larvae of *Papilio machaon* by the great tit *Parus major*. Oikos 36:267–272.

LAUDER, G. V. 1990. Functional morphology and systematics: studying functional patterns in an historical context. Ann. Rev. Ecol. Syst. 21:317–340.

LEDERHOUSE, R. C. 1990. Avoiding the hunt: primary defenses of lepidopteran caterpil-
lars, pp. 175–189. *In* Evans, D. L. & J. O. Schmidt (eds.), Insect defenses. SUNY
Press, Albany.
LESLIE, A. J. & M. R. BERENBAUM. 1990. Role of the osmaterial gland in swallowtail lar-
vae (Papilionidae) in defense against avian predators. J. Lepid. Soc. 44:245–251.
MILLER, J. S. 1987. Phylogenetic studies in the Papilioninae (Lepidoptera: Papilionidae).
Bull. Amer. Mus. Nat. Hist. 186:365–512.
MILLER, J. S. & J. W. WENZEL. 1995. Ecological characters and phylogeny. Ann. Rev.
Entomol. 40:389–415.
MINNO, M. C. & T. C. EMMEL. 1992. Larval protective coloration in swallowtails from
the Florida Keys (Lepidoptera: Papilionidae). Trop. Lepid. 3:47–49.
MUNROE, E. G. 1961. The classification of the Papilionidae (Lepidoptera). Can. Ento-
mol. (suppl.) 17:1–51.
MÜLLER, F. 1879. *Ituna* and *Thyridia*; a remarkable case of mimicry in butterflies. Proc.
Ent. Soc. Lond. 1879:xx–xxix.
NICHOLLS, C. N. & R. JAMES. 1996. Host selection and juvenile survivorship in the swal-
lowtail butterfly *Papilio machaon britannicus* (Lepidoptera: Papilionidae). Entomol.
Gaz. 47:71–86.
POOLE, R. W. 1970. Convergent evolution in the larvae of two *Penstemon*-feeding
geometrids (Lepidoptera: Geometridae). J. Kansas Entomol. Soc. 43:292–297.
POULTON, E. B. 1884. Notes upon, or suggested by, the colours, markings, and protective
attitudes of certain lepidopterous larvae and pupae, and of a phytophagous hy-
menopterous larva. Trans. Entomol. Soc. Lond. 1884:48–58.
————. 1885. Further notes upon the markings and attitudes of lepidopterous larvae, to-
gether with a complete account of the life-history of *Sphinx ligustri* and *Selenia illu-
naria* (larvae). Trans. Entomol. Soc. Lond. 1885:281–329.
————. 1887. The experimental proof of the protective value of colour and markings in in-
sects in reference to their vertebrate enemies. Proc. Zool. Soc. London 1887: 191–274.
ROTHSCHILD, M. 1975. Remarks on carotenoids in the evolution of signals, pp. 20–51.
In Gilbert, L. E. & P. H. Raven (eds.), Coevolution of animals and plants. Univ. Texas
Press, Austin.
RUITER, L. DE. 1952. Some experiments on the camouflage of stick caterpillars. Behav-
iour 4:222–232.
SHEPPARD, P. M. 1960. Natural selection and heredity, 2nd ed. Harper Torchbooks, New
York.
SILLÉN-TULLBERG, B. 1988. Evolution of gregariousness in aposematic butterfly larvae:
a phylogenetic analysis. Evolution 42:293–305.
————. 1990. Do predators avoid groups of aposematic prey? An experimental test.
Anim. Behav. 40:856–860.
SLATER, J. W. 1877. On the food of gaily-coloured caterpillars. Trans. Ent. Soc. Part
III:205–209.
SPERLING, F. A. H. 1987. Evolution of the *Papilio machaon* species group in western
Canada (Lepidoptera: Papilionidae). Quaest. Entomol. 23:198–315.
SPERLING, F. A. H. & P. P. FEENY. 1995. Umbellifer and composite feeding in *Papilio*:
phylogenetic frameworks and constraints on caterpillars, pp. 299–306. *In* Scriber, M.,
Tsubaki, Y. & R. Lederhouse (eds.), Swallowtail butterflies: their ecology and evolu-
tionary biology. Scientific Publishers, Gainesville, Florida.
SPERLING, F. A. H. & R. G. HARRISON. 1994. Mitochondrial DNA variation within and
between species of the *Papilio machaon* group of swallowtail butterflies. Evolution
48:408–422.
STERMITZ, F. R., D. R. GARDNER & N. MCFARLAND. 1988. Iridoid glycoside sequestra-
tion by two aposematic *Penstemon*-feeding geometrid larvae. J. Chem. Ecol.
14:435–441.
TAKAGI, M., Y. HIROSE & M. YAMASAKI. 1995. Antipredator defense in *Papilio* larvae: ef-
fective or not?, pp. 85–92. *In* Scriber, J. M., Tsubaki, Y. & R. C. Lederhouse (eds.),
Swallowtail butterflies: their ecology and evolutionary biology. Scientific Publishers,
Gainesville. Florida.

TINBERGEN, L. 1960. The natural control of insects in pine-woods. I: Factors influencing the intensity of predation by songbirds. Arch. Neerl. Zool. 13:266–336.

TURNER, J. R. G. 1984. Mimicry: the palatability spectrum and its consequences, pp. 141–161. *In* Vane-Wright, R. I. & P. R. Ackery (eds.), The biology of butterflies, 2nd ed. Princeton Univ. Press, Princeton, New Jersey.

TYLER, H. A., K. S. BROWN JR. & K. H. WILSON. 1994. Swallowtail butterflies of the Americas. Scientific Publishers, Gainesville, Florida.

VAUGHAN, F. A. 1983. Startle responses of blue jays to visual stimuli presented during feeding. Anim. Behav. 31:385–396.

WENZEL, J. W. 1992. Behavioral homology and phylogeny. Ann. Rev. Ecol. Syst. 23:361–381.

WIKLUND, C. & T. JÄRVI. 1982. Survival of distasteful insects after being attacked by naive birds: a reappraisal of aposematic coloration evolving through individual selection. Evolution 36:998–1002.

WIKLUND, C. & B. SILLÉN-TULLBERG. 1985. Why distasteful butterflies have aposematic larvae and adults, but cryptic pupae: evidence from predation experiments on the monarch and the European swallowtail. Evolution 39:1155–1158.

WILLIAMS, G. C. 1966. Adaptation and natural selection. Princeton Univ. Press, Princeton, New Jersey.

ANDREW V. Z. BROWER, *Department of Entomology, Oregon State University, Corvallis, Oregon 97331, USA,* AND KAREN R. SIME, *Department of Entomology & Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853, USA.*

FIELD OBSERVATIONS ON MATING BEHAVIOR AND PREDATION OF *HEMILEUCA ELECTRA* (SATURNIIDAE)

Additional key words: visual cues, predation, silk moth, mate location, pheromones.

Hemileuca electra (Wright), the Electra Buckmoth, is a widespread inhabitant of xeric habitats in the southwestern United States and northwestern Mexico (Tuskes 1984). Larvae emerge from diapausing egg masses in the spring and feed on Flat-top Buckwheat, *Eriogonum fasciculatum* Bentham (Polygonaceae) (Stone & Smith 1990). The species is univoltine, flying in autumn, with peak emergence from September through early November (Tuskes & McElfresh 1995). Most adults emerge the same year they pupate; however, reared individuals from San Diego County, California have emerged four and one half years after pupation (pers. obs., Powell 1987). Adults are diurnal, non-feeding, and brightly colored (Ferguson 1971, Tuskes et al. 1996). Mate location is facilitated by an airborne pheromone from 'calling' females, and once a female has mated, she stops releasing the pheromone (Tuskes et al. 1996). While investigating aspects of patch-size distribution of this species in southern California, I observed previously unreported mating behavior, on which I report here.

Field work was conducted between 1030 and 1530 PST, 6–19 October, 1996, at Naval Air Station Miramar (parcel G) in San Diego County, California. 11 mm long rubber lures infused with a chemical blend that replicates the primary components of *Hemileuca electra* female pheromone (Jocelyn Millar & Steve McElfresh, unpubl. data) were deployed to attract conspecific males. The dull red-brown lures were kept in a cooler until trials began. In order to observe male response only to their physical presence, two non-calling, sedentary females that had mated on an earlier day were placed approximately 12 cm from the lures on a flat surface. Fifteen males were allowed to land unmolested on the flat sur-